
SPECIES BEFORE SPECIATION IS COMPLETE¹

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ABSTRACT

The adaptive radiation of Darwin's finches in the Galapagos archipelago stands as a model of species multiplication. The radiation began two to three million years ago, and resulted in 14 species being derived from the original colonizing species. This system is highly suitable for investigating the causes of speciation because closely related species occur sympatrically in several combinations and in environments with relatively little anthropogenic disturbance. The role of natural selection and adaptation to feeding niches in the allopatric phase of speciation has been demonstrated repeatedly. In the sympatric phase of speciation, differences in song and morphology act as a premating barrier to gene exchange. This form of reproductive isolation evolves at least partly as a passive consequence or byproduct of adaptive divergence in beak morphology. Song characteristics diverge in allopatry, largely independent of beak morphology and for a variety of reasons, not all of which are well understood. The barrier to gene exchange in sympatry is not completely effective, however; species hybridize rarely, and under some circumstances the hybrids are surprisingly fit. These results challenge some current notions of species. For example, the ground finch species *Geospiza scandens* Gould and *G. fortis* Gould on the island of Daphne Major have lost morphological diagnosability, as a result of introgressive hybridization, while retaining vocal diagnosability. Speciation is a process of divergence, and therefore these two populations are currently despeciating. With a change in climatic conditions they are expected to respeciate. Such merge-and-diverge dynamics may occur frequently in hybrid zones and in relatively young radiations in habitats subject to strong environmental fluctuations.

Key words: allopatric divergence, conservation, evolutionary potential, hybrid fitness, imprinting, introgression, song, species barrier, species concept.

Two inter-related questions in evolutionary biology have been discussed intensively in the last decade. These are: what are species, and what role does hybridization play in speciation? The debate about species is about concepts and criteria (Coyne & Orr, 2004; de Queiroz, 1998, 2000; Harrison, 1998; Hey, 2001; Mayr, 2000, 2001; Orr, 2001; Shaw, 2001; Wu, 2001a, b). The debate about hybridization centers on whether it has a creative role in speciation through enhancement of multilocus genetic variation, or whether it has no effect or even retards or reverses the process (Mayr, 1942; Stebbins, 1950; Svärdson, 1970; Meham, 1975; Raven, 1976; Arnold, 1997; Hercus & Hoffmann, 1999; Barrier et al., 2001; Barton, 2001; Martinsen et al., 2001; Ortíz-Barrientos et al., 2002; Rieseberg et al., 2003). The two subjects are inter-related because when populations hybridize, and therefore are not completely isolated reproductively from each other, the question arises as to whether they should be considered as one species or two.

We address the two issues of species and hybridization by discussing recent findings from field studies of Darwin's finches on the Galapagos islands. The studies are designed to investigate the causes of speciation within the broader context of an adaptive

radiation. One key component is adaptive divergence in resource (food) exploiting traits. Three major lines of evidence demonstrate the role of natural selection in divergence (P. R. Grant & B. R. Grant, 1997a). First, populations differ ecologically on different islands that have different arrays of food resources (Abbott et al., 1977; Smith et al., 1978). Second, the particular species on an island and their beak sizes are predictable to a large extent from the food supply (Schluter & Grant, 1984). Third, when the food environment changes, evolutionary change occurs as a result of natural selection on heritable variation in beak size and shape as well as body size (Boag & Grant, 1981; B. R. Grant & P. R. Grant, 1989; P. R. Grant & B. R. Grant, 1995, 2002a).

A second key component is divergence in courtship signals and responses leading to reproductive isolation of two populations derived from one. This is the focus of our article. We address four questions: what constitutes a barrier to gene exchange between closely related species, how does it originate, how might it be breached, and what are the consequences of occasional hybridization? Answers to these questions constitute the background to a concluding discussion of species as taxonomic units.

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THE BARRIER TO GENE EXCHANGE

Darwin's finch species are similar in the type of nest they build and, as far as we can tell, in their courtship behavior (Lack, 1947; Ratcliffe & Grant, 1983a). Species in the same genera are similar in plumage but differ in beak morphology and song (P. R. Grant, 1999). Differences in these latter two traits would appear to be the best candidates for barriers to gene exchange and, indeed, field experiments with sympatric species in the ground finch genus *Geospiza* Gould have confirmed their potential role (Ratcliffe & Grant, 1983a, 1985).

The two sets of traits are interestingly different. Beak size and body size are polygenic traits that display high heritabilities (P. R. Grant & B. R. Grant, 2000; Keller et al., 2001), whereas songs, sung only by males, are culturally transmitted from father to son (B. R. Grant & P. R. Grant, 1996a). Bowman (1983) demonstrated with lab experiments that songs of Darwin's finches are learned, in an imprinting-like manner, between approximately day 10 and day 30 after hatching. These 20 days cover the period from the last few days in the nest to the end of the fledglings' dependence on their parents. The father sings throughout this time. Our field studies support Bowman's laboratory findings (B. R. Grant & P. R. Grant, 1989; Gibbs, 1990). They show that a strong resemblance exists between song characteristics of sons and fathers and even paternal grandfathers but not maternal grandfathers (B. R. Grant & P. R. Grant, 1996a).

Often exceptions are more revealing than the rule. Imprinted traits, being learned, are subject to misimprinting if young birds are exposed to the song of a different species rather than, or more than, the father's song, during the short sensitive period of learning. This has been observed in a study of *Geospiza fortis* Gould (medium ground finch) and *G. scandens* Gould (cactus finch) on the small island of Daphne Major (B. R. Grant & P. R. Grant, 1996a, 1998; P. R. Grant & B. R. Grant, 1997b). Misimprinting happens rarely, in three types of circumstances. It occurs when (1) a father dies and the offspring learn the song of the nearest natal neighbor, which can be the bird of another species; (2) nests of two species are close together and one male sings louder, more persistently, and chases off the other male; and (3) a nest with one of the original eggs in it is taken over by a pair belonging to another species, the egg hatches, and the nestling is fed by and learns the song of its foster father.

INTROGRESSIVE HYBRIDIZATION

Following the fates of 16 misimprinted finches has revealed that they mate mainly according to song type

and not morphology, and consequently hybridize and produce hybrid offspring. If they are males, they sing the same single song as sung by their fathers and mate with a female whose father sang that song type (P. R. Grant & B. R. Grant, 1997c). If they are females, they choose a mate that sings the same song as their fathers'. Even though F₁ hybrids and backcrosses are morphologically intermediate between the parental species, they breed strictly according to song type (B. R. Grant & P. R. Grant, 1998). Thus, through occasional misimprinting, introgression of genes occurs in both directions between *Geospiza fortis* and *G. scandens*.

HYBRID FITNESS

Hybrids have been formed rarely (~1% of breeding pairs are interspecific), but approximately continuously, throughout our 30-year study on Daphne Major. However, in the first 10 years none survived to breed. At this time we considered two possible reasons for their failure: genetic incompatibility and ecological insufficiency. Few birds, hybrids and non-hybrids, survived the generally poor feeding conditions in the early years. Hybrids, with their intermediate beak sizes, were unable to crack the large and hard seeds of *Tribulus cistoides* (L.) that the more robust-billed *Geospiza fortis* were feeding on, and they took significantly longer to crack open the seeds of *Opuntia echios* Howell, which is the main dry-season food of *G. scandens* (B. R. Grant & P. R. Grant, 1996b). After the unprecedentedly high rainfall in the El Niño year of 1983, the ecological conditions on the island changed dramatically (P. R. Grant et al., 2000b). The previously common large and hard seeds of *T. cistoides* and *O. echios* diminished in the seed bank, these plants having been smothered by vines and other small-seed producing plants. Under these altered conditions of an abundance of small and soft seeds, hybrids and backcrosses survived to reproduce. Therefore, their previous failure is attributable to ecological insufficiency and not to genetic incompatibility.

After 1983, hybrids survived as well as, if not better than, their parental species, and reproduced as well as them, there being no difference in number of eggs, nestlings, or fledglings produced (P. R. Grant & B. R. Grant, 1992). We detected no loss of fitness in the F₁ and backcross generations in terms of relatively poor survival, mating success, or reproduction (P. R. Grant & B. R. Grant, 1992; B. R. Grant & P. R. Grant, 1998; P. R. Grant et al., 2003; but see Barton, 2001).

IMPLICATIONS OF INTROGRESSION

There are two important implications of the documented introgressive hybridization. First, post-

mating isolation appears not to have evolved between these and other pairs of ground finch species (B. R. Grant & P. R. Grant, 1989, 1998; P. R. Grant et al., 2005). Even more distantly related species of Darwin's finches have been known, or suspected, to hybridize without a recorded loss of fitness (P. R. Grant, 1999). This is not surprising. According to comparative evidence from other bird species it takes more than two million years for post-zygotic incompatibilities to evolve (Price & Bouvier, 2002). All, or almost all, of the adaptive radiation of Darwin's finches took place in less than this time (P. R. Grant, 1999; Sato et al., 2001; Burns et al., 2002). Second, hybridization and backcrossing has enhanced the evolutionary potential of these two species by increasing additive genetic variances while reducing constraints from genetic correlations (P. R. Grant & B. R. Grant, 1994). The reduction in strength of genetic correlations between beak size traits is due to the interspecific differences in allometries. In principle, a third implication is that hybrids have the potential to invade new habitats (Lewontin & Birch, 1966) and even form a new species in another environment (see Rieseberg, 2006 this issue). We conjecture that introgressive hybridization may have contributed to speciation in the past, although we lack evidence that this happened in any particular case.

THE ORIGIN OF A BARRIER TO GENE EXCHANGE

Based on these findings, reproductive isolation of Darwin's finches is explained by a theory of discrimination by song in association with morphology that is learned in a sexual imprinting-like process early in life (B. R. Grant & P. R. Grant, 2002; P. R. Grant & B. R. Grant, 2002b).

We now apply contemporary findings from Daphne to the question of how reproductive isolation evolves, using as a framework the allopatric model of speciation. The model invokes ecological adaptation in allopatry as a requirement for the establishment of sympatric coexistence of two species derived from one. For this there is plenty of evidence (see introduction to this article). A total or near-total lack of interbreeding is another requirement. The model invokes an allopatric origin of a pre-mating barrier to gene exchange. Experiments show that some degree of differentiation in the cues used in mate choice must arise allopatrically.

Experiments with museum specimens from different islands were conducted to simulate the secondary contact phase of the speciation cycle (Ratcliffe & Grant, 1983b). In a variety of tests with different ground finch species, we consistently found weak or

no discrimination between an immigrant and a (resident) member of the responding bird's own population when beak differences between them were small, and strong discrimination when the differences were large. Acoustic cues were controlled for in these experiments by eliminating them; dead museum specimens do not sing!

Playback experiments without museum specimens as visual cues showed that ground finches discriminate acoustically between residents and immigrants in a similar way to their visual discrimination: they discriminate when differences are large and fail to do so when they are small (Ratcliffe & Grant, 1985).

The morphological barrier arises as a result of adaptation. As such it conforms to an old idea dating back at least 65 years to Dobzhansky (1937) that reproductive isolation originates as a byproduct of adaptive differentiation. We know less about how the song barrier arises (B. R. Grant & P. R. Grant, 2002; P. R. Grant & B. R. Grant, 2002b). One possibility is that song characteristics covary with beak size for biomechanical reasons, affecting trill rate and the range of frequencies of individual notes (Podos, 1997) and, therefore, when beak size changes adaptively, songs change as a passive consequence. There is some supporting evidence (Podos, 2001); nevertheless, correlated effects of beak change appear to be insufficient to set up a barrier to gene exchange because coexisting sister species of *Geospiza* do not differ discretely in these two song features (B. R. Grant & P. R. Grant, 2002). In contrast to this interspecific similarity, populations of the same species may differ substantially in songs independent of beak size differences (P. R. Grant et al., 2000a). The hypothesis is undermined by the ability of sympatric species with different beak sizes to sing each other's songs with scarcely altered characteristics (Bowman, 1983; B. R. Grant & P. R. Grant, 1989, 1998; P. R. Grant & B. R. Grant, 1997b, c). Correlated effects of body size changes may also contribute to a barrier through an influence on frequency characteristics of songs (Bowman, 1983). Since beak size and body size generally covary, a third, and more realistic, hypothesis is that they are jointly involved in determining characteristics of songs and hence the barrier to interbreeding. Another possibility is that a new song type may originate as a cultural mutation through miscopying of father's song and increases in frequency by chance or selectively. A selective advantage may arise if the songs transmit better in the new environment and, as a result, more effectively repel intruding males or attract females. The origin of reproductive isolation is still not fully understood, and these possibilities need further investigation.

ADAPTIVE DIVERSIFICATION THROUGH REPEATED SPECIATION

The foregoing explanation of how two species are formed from one serves as a basis for explaining the adaptive radiation as a whole (P. R. Grant & B. R. Grant, 2002c). Fourteen species evolved from a single ancestral species by a simple repetition of the process of division, with the species produced at each step differing according to the particular ecological circumstances that guided each pathway. This was our starting point (P. R. Grant, 1981, 1999). Furthermore, we believed most niche space would be occupied in the early history of the radiation, with later speciation resulting in gap-filling, as illustrated recently by Jonathan Losos and colleagues with Caribbean *Anolis* Daudin lizards (Harmon et al., 2003; Losos et al., 2006 this issue). For experimental and observational work we concentrated on the ground finch twigs of the phylogenetic tree, because these species are most similar to each other and have been genealogically separated for a short time. To see if the same processes of divergence in morphology and song occurred early in the history of the radiation, we have gone to the base of the tree. There, five years ago, we encountered a surprising fact. The initial divergence is frozen at the allopatric stage. Reconstructions that have used both mitochondrial and nuclear genetic markers (Freeland & Boag, 1999a, b), including microsatellite DNA (Petren et al., 1999), show a basal split between two groups of warbler finches that are now allopatric on different sets of islands (Petren et al., 1999; Tonniss et al., 2005).

Why have they remained allopatric? What has prevented them from establishing sympatry? We do not have complete answers to these questions. Part of any answer requires greater knowledge than we have of ecological opportunity for joint occupancy of an island. Another part requires knowledge of potential reproductive isolation, and this we do have.

Morphologically the two groups of warbler finches are similar; correspondingly, they are similar ecologically as well. They also share the peculiar feature of reversed sexual dimorphism in beak length, in which trait they differ from all other Darwin's finch species and from all continental relatives (P. R. Grant & B. R. Grant, 2003). They differ from each other to some extent in plumage color and beak size, but scarcely enough to prevent them from interbreeding to judge from differences in pairs of sympatric species of Darwin's finches. However, their songs do differ (B. R. Grant & P. R. Grant, 2002). With a focus on the question of the origin of reproductive isolation, we performed a set of playback experiments similar to earlier ones in which we simulated immigration of birds from another island (B. R. Grant & P. R. Grant,

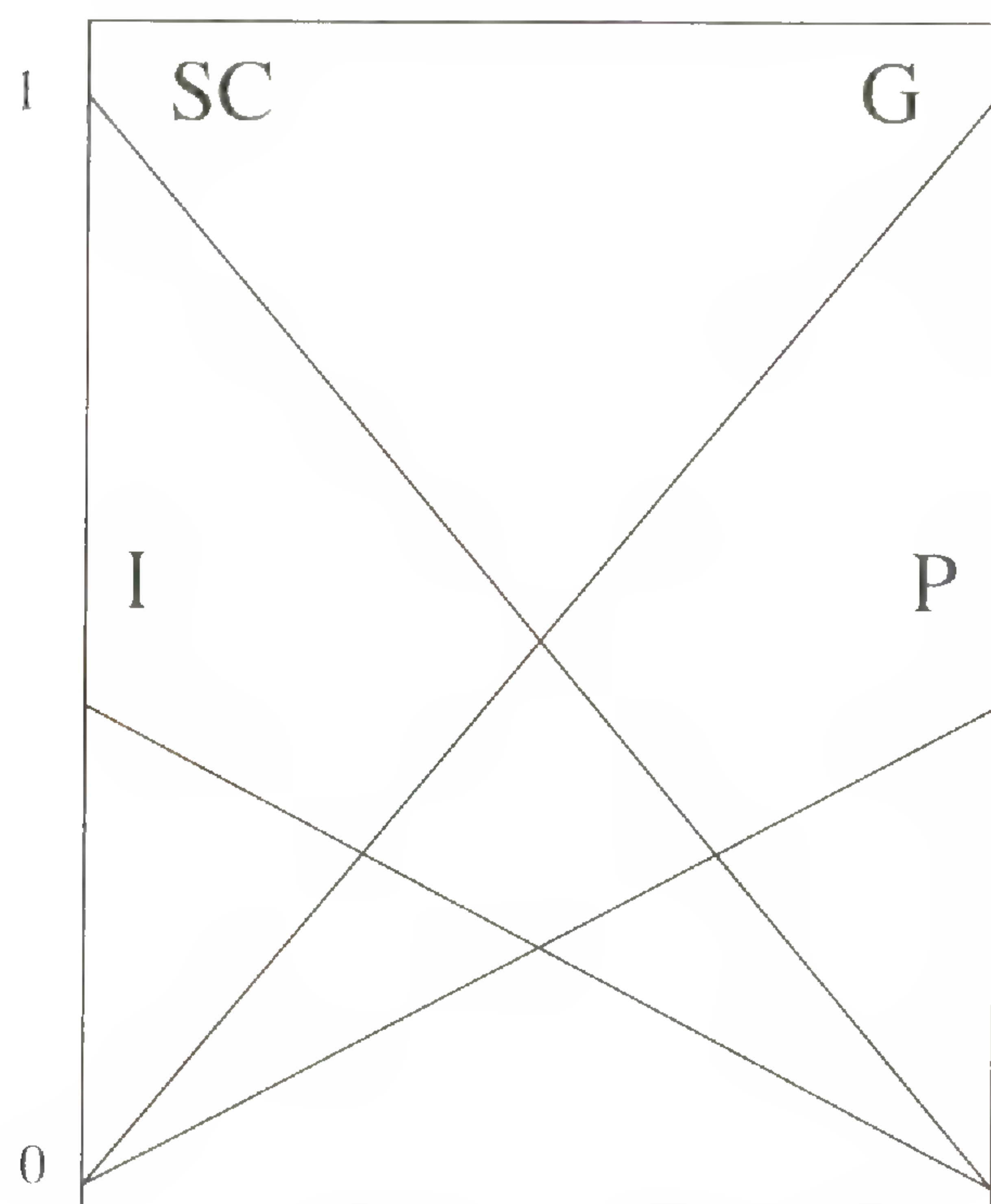
2002; P. R. Grant & B. R. Grant, 2002c). On the island of Genovesa, occupied by *Certhidea fusca* Sclater, we tested birds with their own songs, songs from another population of *C. fusca*, and songs from two populations of *C. olivacea* Gould. We performed similar experiments with the same playback tapes on an island, Santa Cruz, occupied by *C. olivacea*. We expected to find strong discrimination, manifested in the pattern of contrasts shown in Figure 1 (above). Instead we found little evidence of discrimination of heterotypic (heterospecific) song on either island (Fig. 1, below). This is fascinating because it contrasts with clear discrimination between sympatric and younger species. One would have thought warbler finches of the two groups have surely had enough time to diverge in both beak morphology and song to enable them to coexist without interbreeding. Yet the implication of the playback results is that the oldest (allopatric) lineages would interbreed, whereas the youngest (sympatric) ones do not, or do so very rarely. Moreover, the genetic evidence tells us that despite their apparent potential to exchange genes, they have not done so, at least not to an appreciable extent, for a long time (Petren et al., 2005).

There are three other implications of this striking contrast (B. R. Grant & P. R. Grant, 2002). The first is that rates of song and morphological divergence vary among the species; hence, the rate of evolution of sexual isolation varies considerably and is not a simple function of time. The second is that either divergence in song is accelerated in sympatry, perhaps by selective reinforcement of initial differences if offspring of mixed matings are at a selective disadvantage, or establishment of sympatry is made possible only by the acquisition of pronounced song differences in allopatry. The third implication is that a knowledge of neutral genetic differences among taxa in young radiations like Darwin's finches is not enough for inferring their potential to interbreed and exchange genes. Geographical, ecological, and behavioral information is needed as well (Petren et al., 2005; Tonniss et al., 2005). Ferguson (2002) has argued similar points more generally.

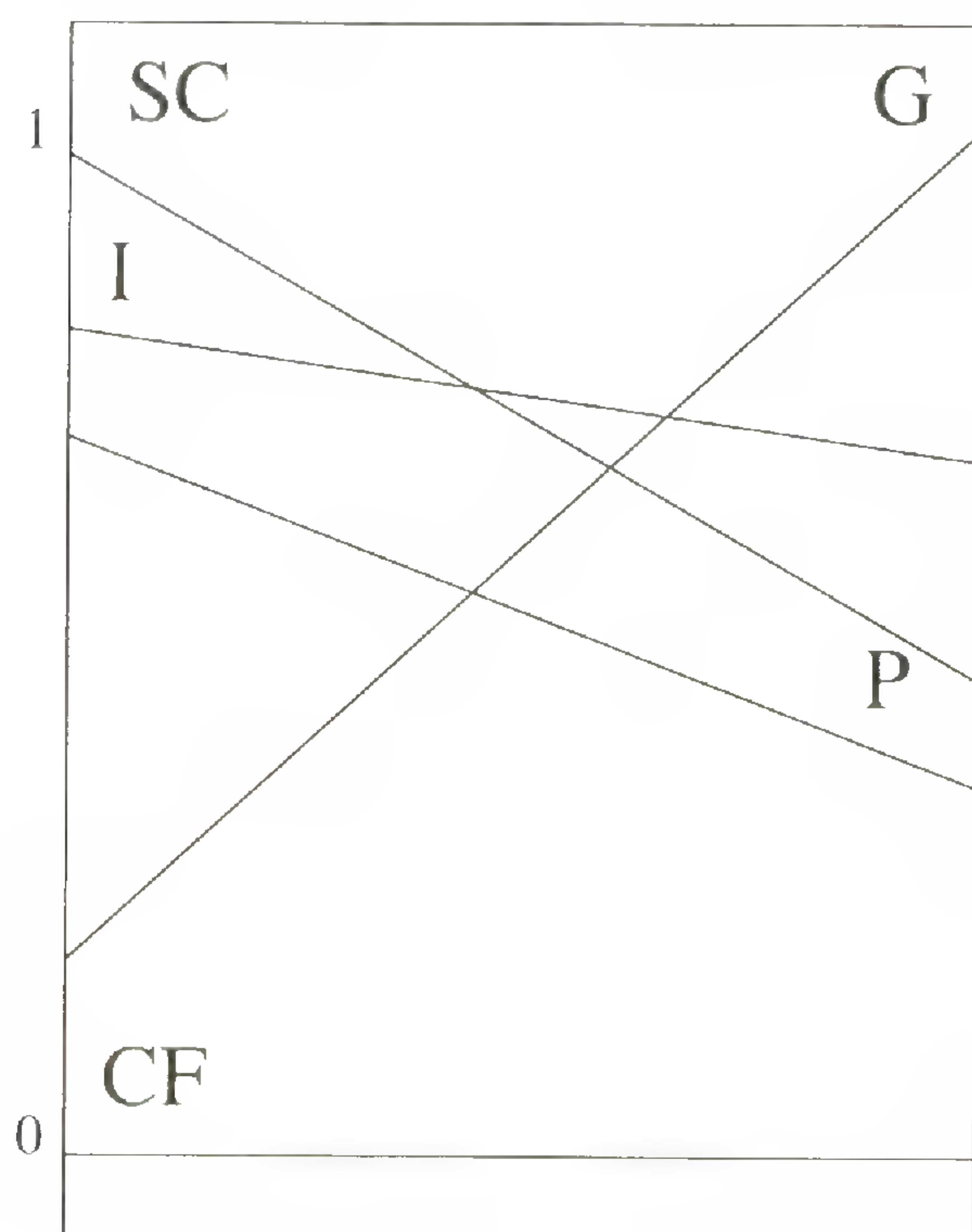
SPECIES RECONSIDERED

According to Cracraft (2002), the first great question of systematic biology is, what is a species? Templeton (1989) has suggested this question must be answered before the process of species formation can be investigated. Like other evolutionary biologists attempting to understand speciation, we have not heeded this advice. Instead of defining the species we study, we have found it sufficient to simply invoke the biological species concept with its emphasis on the

Expected Response to Playback



Observed Response to Playback



C. olivacea

C. fusca

Santa Cruz

Genovesa

Figure 1. Expected (above) and observed (below) responses of warbler finches on Santa Cruz (*Certhidea olivacea*) and Genovesa (*C. fusca*) to playback of songs recorded on Santa Cruz (SC), Isabela (I), Genovesa (G), and Pinta (P). Responses are scaled to 1.0 on each island where experiments were conducted. Controls were Cassin's finch (CF) songs recorded in North America. Populations on Santa Cruz and Isabela belong to the *C. olivacea* lineage, and populations on Genovesa and Pinta belong to the *C. fusca* lineage. Figure based on B. R. Grant & P. R. Grant, 2002: fig. 3 (© 2002 by the University of Chicago).

evolution of reproductive isolation and not on classification (Harrison, 1998; Hudson & Coyne, 2002). De Queiroz (1998: 63) has followed the paleontologist G. G. Simpson (1961) in arguing "there is really only one general species concept in modern systematic and evolutionary biology—species are segments of population level evolutionary lineages." He then offers an important distinction: "A *species concept* is an idea about the kind of entity represented by the species category, that is, about the kind of entity designated by the term *species*. A *species criterion* is a standard for judging whether a particular entity qualifies as a member of the species category, that is, for judging whether a particular entity is or is not a species" (de Queiroz, 1998: 65). This neatly bypasses the plethora of tangled arguments about species concepts and allows debate to be focused on how species should be recognized.

Ernst Mayr (1942) defined species as groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such populations. The criterion here is clearly one of interbreeding. Application of this definition to individuals in order to refer them to species has repeatedly encountered practical difficulties with allopatric populations and with populations connected occasionally or rarely by interbreeding (Zink & McKittrick, 1995; see Avise & Wollenberg, 1997, and Wake, 2006 this issue). These practical difficulties have been faced head-on by ornithological systematists. For example, the Taxonomic Subcommittee of the British Ornithologists' Union confronted them in drawing up guidelines to assist in the assessment of species rank for the British Bird Species List. They started with a position statement: "If we define species as population lineages maintaining their integrity with respect to other such lineages through time and space, this means that species are diagnosably different (otherwise we could not recognize them), reproductively isolated (otherwise they would not maintain their integrity upon contact) and members of each (sexual) species share a common mate recognition and fertilization system (otherwise they would be unable to reproduce)" (Helbig et al., 2002: 519). Then they followed with two recommendations. First, "Diagnosable taxa will be ranked as species if they are broadly sympatric, i.e., over areas beyond the average natal dispersal distance of the species involved, . . . and do not hybridize, . . . or hybridize only rarely, so that gene flow between them either does not occur (because hybrids are sterile or do not backcross for other reasons) or occurs at such a low frequency (often difficult to detect) that it is unlikely their gene pools will ever merge, . . ." (Helbig et al., 2002: 522). Second, allopatric populations

should be considered different species “if they have diverged to the extent that merging of their gene pools in the future is unlikely” (Helbig et al., 2002: 519), whereas, “predictions about possible reproductive isolation between allopatric taxa that differ only slightly (e.g., in size or darkness of plumage) are very uncertain. Such taxa are best treated as subspecies” (Helbig et al., 2002: 519). On the basis of the latter, and recognizing our ignorance of post-mating compatibility, the warbler finches are best treated as subspecies. We consider them to be well-differentiated genetic lineages.

These prescriptions for sympatric and allopatric species fit very well with our past 30 years of thinking and practice based on the biological species concept and notwithstanding the fuzziness (Harrison, 1998; Hey, 2001; Lee, 2003) of species boundaries caused by rare hybridization. The prescriptions clearly apply to sexually reproducing species generally and not just to birds. Nevertheless Darwin’s finch studies expose two hidden problems with the diagnosis of sympatric species. First, species may lose diagnosability. Second, if they do it is an arbitrary matter to decide when they lose their species status.

At the beginning of our study on Daphne Major *Geospiza fortis* and *G. scandens* were diagnosably different on morphological criteria (P. R. Grant, 1993). With hybridization, backcrossing, and natural selection occurring, the populations have converged in morphology and are now more similar than they were at the beginning (P. R. Grant & B. R. Grant, 2002a; P. R. Grant et al., 2004). They are no longer 100% diagnosably different on the same morphological criteria. Have they lost their species status in a couple of decades? They are merging, but very slowly. Members of the two populations can still be recognized by us on the basis of the song they sing (males) or the song of their mates (females), as well as by beak morphology in almost all instances. The problem that this poses for the delineation of species is that song is a learned, culturally inherited, trait, without a genetic basis in many species of birds, and yet “...characters used in diagnosis must be the result of evolution: they must be genetically based and not merely caused by environmental factors such as nutrition” (Helbig et al., 2002: 520). A way out of this dilemma is to broaden the basis of diagnosis by recognizing that cultural inheritance may be as important as genetic inheritance in trans-generational maintenance of biologically important traits used in reproduction. We recommend this because song is the cultural equivalent of the Y chromosome in these birds; paternally inherited, non-recombining, and subject to change only by mutation, cultural mutation in this case. Song variation has been found to be

useful in systematic studies of other groups of birds (Ahlström & Ranft, 2003).

The second problem has no simple solution. “We do not know of a single documented case of breakdown of reproductive isolation (i.e., a reversal to full reproductive compatibility between species that were incompatible before) in any class of organism” (Helbig et al., 2002: 521). However, Kat (1985) described a possible case of breakdown of reproductive isolation with two species of *Anodonta* L. freshwater mussels. According to fossil evidence, they coexisted without interbreeding about 200,000 years ago, and now at the same locality they hybridize relatively commonly. The two finch species on Daphne may become the first exception to be witnessed in progress. At present they are on a reversed course of speciation (P. R. Grant et al., 2004), in fact they are *despeciating*, and the point at which they should no longer be considered two species, but only one, is arbitrary. Morphological and genetic convergence could easily be reversed if there is a change in climate and food composition, in which case they will be *respeciating*. Many other pairs of taxa, not just Darwin’s finches, might go through similar merge-and-diverge oscillations, as in some shifting hybrid zones (e.g., Carney et al., 2000), possibly also in young adaptive radiations such as the silversword alliance in Hawaii (Barrier et al., 2001; Baldwin, this volume) and cichlid fish in the African Great Lakes (Salzburger et al., 2002; Smith & Kornfield, 2002).

Such fluidity can be bewildering to those who recognize species by inferred ancestry rather than by interbreeding and its consequences. For instance Zink (2002), basically restricting attention to the lack of differentiation in mitochondrial DNA among species (Freeland & Boag, 1999a, b; Sato et al., 1999) that are upheld by other criteria, has argued there are far fewer species of Darwin’s finches than are currently recognized, perhaps only half. Aside from an unfortunate reliance on a single, potentially misleading, molecule (Ballard et al., 2002; Hudson & Coyne, 2002; Ferguson, 2002; Machado & Hey, 2003; Rokas et al., 2003), a view such as this overlooks the fact that as many as 10 species coexist on the same island, ecologically differentiated, morphologically recognizable, and reproductively isolated by song and morphology (P. R. Grant, 1999).

These problems illustrate the well known fact that systematics deals with discrete categories, whereas evolutionary change is a continuous and gradual process (Harrison, 1998; Hey, 2001; Hey et al., 2003). Darwin’s finches are valuable to evolutionary biologists precisely because they so well exemplify the graded nature of evolutionary transitions. They are challenging to systematists for the same reason.

CONSERVATION OF BIODIVERSITY

Darwin's finches are valuable to conservation biologists for another reason. They deliver a message about preserving biodiversity: since species, like their environments, are continually changing, both must be conserved to allow adaptation to further change. For any given focal species, or evolutionarily significant population of the species (Hey et al., 2003), other species in the community are part of the environment, be they food, competitors, predators, or parasites. This is especially clear in the case of interbreeding species, because their ecological and evolutionary future depends to some extent upon the genes they exchange with each other (Cade, 1983; B. R. Grant & P. R. Grant, 1989; Rhymer & Simberloff, 1996). It is clear with competitor species that persist only when predators prevent one species from competing the others to extinction (Paine, 2002). It is clear from the dependence of finches (B. R. Grant & P. R. Grant, 1989) and primates (Terborgh, 1983) on one or two specific food sources at seasons of acute food limitation. And it is clear from the myriad indirect effects that are manifested in the trophic networks of complex communities (e.g., Wootton, 1993; Dayton, 2003). Thus ecosystems, rather than individual species, are the appropriate units in programs of long-term conservation of biodiversity.

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